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CONVERGENT FLORAL EVOLUTION IN SOUTH AFRICAN AND AUSTRALIAN PROTEACEAE AND ITS POSSIBLE BEARING ON POLLINATION BY NONFLYING MAMMALS

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ABSTRACT

Striking convergent evolution for a hidden (cryptic), ground flowering (geoflorous) habit in distantly related, low shrubby Australian and South African Proteaceae is interpreted as an adaptation for pollination by nonflying mammals. The cryptic, geoflorous habit is especially well developed in species groups of *Dryandra* in southwestern Australia and *Protea* in the Cape region of South Africa. Considerable circumstantial evidence exists in both regions for pollination by mouselike, often arboreal marsupials in *Dryandra* and true rodents in *Protea*. Evidence from inflorescence structure suggests the cryptic, geoflorous habit is derived from bird-pollinated species, possibly in response to fires common in the sclerophyllous communities where these genera grow. A number of floral characteristics and the occurrence in Australia of mouselike marsupials adapted to a nectar (and pollen?) diet suggests that a class of flowers has evolved for pollination by nonflying mammals. This postulated floral class possibly also extends to other Australian arboreal proteaceous and also myrtaceous genera, but in South Africa is probably restricted to *Protea*.

Pollination by nonflying mammals is largely ignored or given little credence in current treatments of pollination ecology (Faegri & van der Pijl, 1971; Proctor & Yeo, 1972). There is, however, good reason for this; all the available evidence relating to this phenomenon is either circumstantial, inferential, or anecdotal.

Nonetheless, field observations in Australia and South Africa and a subsequent search of the literature have led us to believe that true rodents and marsupials may, in fact, be the normal pollinators of several southern hemisphere proteaceous genera. Furthermore, various floral characteristics in these genera and the special adaptations for nectar feeding in some of the putative pollinators suggest structural coadaptations by both flowers and apparent pollinators. Although plans are underway to conduct definitive studies, no unequivocal evidence can be presented at this time for regular pollination by nonflying mammals, and

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that is not the intent of this paper. We hope, however, that our comments will help to reopen and stimulate research in this fascinating area of pollination biology pioneered by Porsch (1934, 1935, 1936a, 1936b) and subsequently neglected for 40 years. The purpose of this paper is fourfold: (1) to elucidate our observations and ideas on inferred pollination by nonflying mammals in the South African and Australian Proteaceae, (2) to point out the striking convergent evolution of flowering habits between southwestern Australian and South African Proteaceae of the Cape region, (3) to review some of the rather scattered and fragmentary literature on the subject, and (4) to evaluate the evidence for the existence of a class of flowers adapted to pollination by nonflying mammals.

References to the subject of pollination by nonflying mammals usually mention the arboreal Australian marsupials which apparently feed on nectar (e.g., the honey possum, *Tarsipes spencerae*) and to introduced rats suspected of pollinating a climbing pandan (*Freycinetia arborea* Gaudich.) in Hawaii. Faegri & van der Pijl (1971) and Proctor & Yeo (1972) furthermore state that no flowers appear to be adapted for pollination by nonflying mammals, although Faegri and van der Pijl mention the classic papers by Porsch (1934, 1935, 1936a, 1936b) in which he builds a case for floral adaptations to pollination by nonflying mammals in several Australian genera. Grant (1950) mentions, without comment, a "marsupial" pollinated flower class based on the proteaceous genus *Dryandra*.

In addition to rodents and mouselike marsupials, some primates may also be regular pollinators. For example, according to Coe & Isaac (1965) the baobab (*Adansonia digitata* L.) is pollinated in East Africa by the lesser bush baby (a loridid primate). This characteristic African tree is generally considered to be bat pollinated. Petter (1962) mentions that several arboreal, mouselike lemurs (*Lemur*, *Varecia*, *Hapalemur*, *Microcebus*) visit flowers seeking nectar and are generally attracted by sweet liquids in captivity. More recently Sussman & Tattersall (1976, and personal communication) demonstrate that *Lemur mongoz* is apparently an important pollinator of introduced kapok (*Ceiba pentandra* Gaertn.) in Madagascar. F. L. Carpenter (personal communication) has data from Australia indicating that some species of *Banksia* are pollinated almost entirely by nonflying mammals, including an indigenous rat (*Rattus fuscipes*) and various marsupials.

It is not our intent to evaluate the entire literature here. There are, however, numerous instances of various mammals being observed on or around flowers (Porsch, 1934), but the nature of their activities are, in fact, virtually unknown. As Faegri & van der Pijl (1971) point out with respect to pollination by nonflying mammals "much research remains to be done to establish relationship between possible regular pollinators and the blossoms in which they work."

FLORAL CHARACTERISTICS AND CONVERGENT EVOLUTION OF PROTEACEAE PUTATIVELY POLLINATED BY NONFLYING MAMMALS

The most obvious Proteaceae are trees and large shrubs, e.g., *Grevillea* and *Banksia* in Australia, and *Protea* in South Africa. Less known, however, is the occurrence of species groups on both these continents with inflorescences at or near ground level (geoflorous) and typically obscured from external view by

overlying foliage (cryptic). The taxonomic distribution of these cryptic, geoflorous species is limited principally to two distinct sections of *Protea* [*Hypoccephalae* and *Microgeantheae*, sensu Phillips (1912)] and some additional species of uncertain sectional classification in the Cape region of South Africa; in southwestern Australia, however, this flowering habit is associated with at least five genera (*Banksia*, *Conospermum*, *Dryandra*, *Isopogon*, and *Petrophile*) but is best developed in *Dryandra* [series *Aphragmia* and *Niveae*, sensu Bentham (1870)] and to a somewhat lesser extent in *Banksia*.

In these equivalent infrageneric groupings in *Protea* and *Dryandra* the growth habit is low, tufted, and often rhizomatous. The flowers occur in heads, usually at ground level, or occasionally up to 30 cm high, but in either case the heads are typically deeply hidden within the foliage of the dense and widely spreading branch systems. The heads are generally visible only if the branches are forcibly parted and the base of the plant carefully examined (Figs. 1–6). The flowers are surrounded by a prominent series of overlapping bracts forming a cup-shaped involucre. The bracts vary in color through various shades of brown and are often flushed with different dull reddish tints. An inflorescence contains perhaps 100–200 flowers, but the large spikes of *Banksia* bear several thousand individual flowers. Many of the species produce copious amounts of nectar and the heads often emit a distinctive, “nutty” or “yeasty” odor. In the cryptic, geoflorous Cape species of *Protea* the basal portions of the bracts and flowers, particularly the styles, are also markedly succulent. Excellent illustrations of *Protea* flowers (but not necessarily the growth habits) can be seen in Rousseau (1970) for South African proteas and in Erickson et al. (1973) for Australian genera.

Dryandra, as in most western Australian Proteaceae, develops no obvious succulence in the inflorescence or flowers. In general, the geoflorous habit, the cryptic positioning of the inflorescences, and the gross (though superficial) morphological similarities of the heads suggest strong convergent evolutionary tendencies. In fact, from a distance one would be hard pressed to distinguish between some species of *Dryandra* and *Protea* even though these genera represent the end points of evolution in two subfamilies of the Proteaceae, Grevilleoideae and Proteoideae, respectively, and occur on widely separated continents (Figs. 1–6).

EVIDENCE FOR RODENT POLLINATION IN SOUTH AFRICAN PROTEAS

Field observations over a period of years of the cryptic, geoflorous species of *Protea* in the Cape area show that considerable rodent activity is associated with these species (Table 1), but is especially obvious in *P. subulifolia*. The specific rodent activities associated with this species are: (1) freshly chewed involucre bracts and styles during and just prior to anthesis (Fig. 7); (2) clearly demarcated networks of heavily used runways linking different plants within populations, and which often intertwine around flowering and old fruiting heads; and (3) occasional burrows at the base of the plants.

The runways and burrows are related to activities of the Cape striped field mouse (*Rhabdomys pumilio pumilio*). On various occasions and in different populations this animal (which is diurnal) was observed on runways between



TABLE 1. The South African species of *Protea* in sections *Hypocephalae* and *Microgeantheae*. All species ground flowering or near ground flowering.

<i>Hypocephalae</i>		<i>Microgeantheae</i>	
<i>P. subulifolia</i> (Salisb. ex Knight) Rourke ^a		<i>P. acaulos</i> (L.) Reichard ^a	<i>P. montana</i> E. Mey. ex Meisn.
<i>P. amplexicaulis</i> R. Br.		<i>P. angustata</i> R. Br.	<i>P. restionifolia</i> (Salisb. ex Knight) Rycroft ^a
<i>P. decurrens</i> Phillips		<i>P. aspera</i> Phillips ^a	<i>P. revoluta</i> Buek ex Meisn.
<i>P. humiflora</i> Andrews ^a		<i>P. cordata</i> Thunb.	<i>P. scabra</i> R. Br. ^a
		<i>P. foliosa</i> Rourke	<i>P. scabriuscula</i> Phillips
		<i>P. glaucophylla</i> Salisb.	<i>P. scolopendrium</i> R. Br.
		<i>P. intonsa</i> Rourke ^a	<i>P. scorzonerifolia</i> Salisb. ex Knight
		<i>P. laevis</i> Thunb.	<i>P. sulfurea</i> Phillips ^b
		<i>P. lorea</i> R. Br. ^b	<i>P. vogtsiae</i> Rourke ^a

^a Species in which evidence of rodent activities has been observed on flowers.

^b Inclusion in this taxonomic section questionable.

flowering plants of *P. subulifolia*. That the Cape striped field mouse is attracted to the cryptic, geoflorous inflorescences of *P. subulifolia* was further demonstrated when it was live-trapped utilizing fresh flowering heads of this species as bait. In this instance traditional rodent baits such as peanut butter were ineffectual in capturing this animal.

The Cape striped field mouse apparently also visits the flowering heads of *Protea nana* (Berg.) Thunb., a low shrubby species with pendulous heads of uncertain pollination type and not a member of the geoflorous sections. The soft floral parts of *P. nana* were chewed in the same manner as *P. subulifolia* and a Cape striped field mouse was trapped at this plant within 24 h of the first noted rodent activity.

The fleshy involucre bracts and styles of the cryptic, geoflorous proteas show widespread evidence of being chewed. In one population of *P. subulifolia* 17 plants bearing 49 inflorescences with open flowers were observed in an area of approximately 30 m²; 20 heads, or 40%, showed extensive evidence of chewed bracts and styles (Cape striped field mice were common in the area). The consistent occurrence of chewed bracts and styles in the cryptic, geoflorous proteas suggests that they function as food bodies; supporting this idea is the sweetness (at least to the human palate) of these structures. In the large, bird-pollinated proteas the bracts not only lack succulence but are markedly acrid, apparently containing high concentrations of tannin. In spite of their sweet, fleshy nature and apparent lack of tannin, all the bracts and mature styles of any head are rarely eaten. That the inflorescences are not completely destroyed suggests the presence of secondary compounds which might limit the amount of feeding as proposed by Freeland & Janzen (1974).

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FIGURES 1-4.—1. General aspect of *Protea subulifolia* just beginning to flower (near Hermanus, Cape Prov., South Africa).—2. Cryptic, geoflorous inflorescences of *P. subulifolia* (same plant as above).—3. General aspect of *Dryandra tenuifolia* in full flower (Stirling Range, West Australia).—4. Cryptic, geoflorous inflorescences of *D. tenuifolia* (same plant as above).

Sweet, fleshy bracts are also associated with pollination in *Freycinetia* (Pandanaeae) where they reportedly attract introduced rats in Hawaii (Degener, 1945) and in other areas of the Pacific (B. C. Stone, personal communication). *Freycinetia insignis* Blume, an Asian bat-pollinated species, apparently utilizes only odor and fleshy bracts as attracting devices (Proctor & Yeo, 1972).

The sense of smell is well developed in rodents, and in view of the hidden nature of the inflorescences, odor must be the primary attracting mechanism regardless of the pollinator. Furthermore, at the time of flowering in *P. subulifolia* (late winter), the fleshy bracts and styles constitute one of the best sources of soft palatable vegetable matter in the local plant community. Thus flowering might correlate with the low point in the food cycle of rodents. The Cape striped field mouse is apparently fond of soft vegetable matter, sometimes becoming a nuisance in vegetable gardens (Roberts, 1951). As further evidence of this dietary habit, newly harvested shoots of another proteaceous shrub, *Leucodendron modestum* Williams, were observed along a typical runway and entrance to a Cape striped field mouse burrow. If the chewing activity in the flowering heads of the Cape species of geoflorous proteas is due to the Cape striped field mouse, or a similar-sized animal, pollen would surely accumulate about the head of the animal and should theoretically be capable of transfer to nearby plants. The fur of mammals should provide an excellent surface for pollen accumulation. This is demonstrated by the presence of pollen on the head of a nectar-feeding Australian marsupial, the sugar glider (*Petaurus breviceps*) (Breedon & Breedon, 1970: inside back cover). An interesting description of pollen accumulation on the Australian honey possum (*Tarsipes spencerae*) feeding on Proteaceae is also given by Vose (1972).

Because of its known association with *Protea* (especially *P. subulifolia*), the Cape striped field mouse is perhaps the best possibility for a mammal pollinator of the cryptic, geoflorous species of *Protea*. However, other rodents in the Cape fauna should also be examined for possible activities relating to pollination. Dr. J. Jarvis of Cape Town University (personal communication) suggests especially the following animals: *Dendromus melanotis* (climbing mouse), *Leggada minutoides* (dwarf mouse), *Otomys irroratus* (vlei otomys), and *Acomys subspinosus* (Cape spiny mouse). None of these animals, however, appear to have any special adaptations for nectar or pollen feeding.

A single case of interspecific hybridization (*P. restionifolia* × *P. humiflora*) is known among the cryptic, geoflorous species of Cape *Protea*. That such a cross occurs is proof that pollen can be transferred between these species. Furthermore, evidence of rodent activity is known in both parental species of the cross. The Proteaceae are apparently adapted for outcrossing and thus require a mechanism for pollen transfer. The family is apparently either protandrous (Rao, 1971) or self-incompatible (Horn, 1962). Pollen dispersal ultimately occurs from a specialized region of the style apex known as the pollen presenter (Rourke, 1969). This is so close to the slitlike stigmatic surface that mechanisms to prevent autogamy must be present or selfing would be the rule and pollination unnecessary.

EVIDENCE FOR MARSUPIAL AND RODENT POLLINATION IN AUSTRALIAN PROTEACEAE

Field observations of the inflorescences of *Dryandra tenuifolia* R. Br. in southwestern Australia also showed evidence of mammal activities similar to those mentioned for *Protea subulifolia* from the Cape region of South Africa; chewed heads were particularly common. The inflorescences were also odoriferous and the scent was surprisingly similar to the "yeastlike" odors prevalent in the cryptic, geoflorous species of African *Protea*. Copious nectar was not detected, but our observations were made in mid-afternoon when nectar content was possibly low. Nectar production in the Australian cryptic, geoflorous Proteaceae may be largely nocturnal to coincide with increased animal activity at that time (Morcombe, 1968). Porsch (1935) repeatedly mentions high nectar production in *Dryandra nivea* R. Br., which he observed under cultivation. He also noted nocturnal anthesis and an odor of "sour milk" or "caraway liquor" in this species. Dr. Alex George (personal communication) has also seen apparent mammal activity in the inflorescences of the cryptic, geoflorous species of *Banksia* where chewing and disturbance of the flowers appeared to be similar to our observations in South Africa. F. L. Carpenter (personal communication) also has interesting evidence that *Banksia* species in eastern Australia are largely pollinated by nonflying mammals. She correlates nonflying mammal pollination in *Banksia* with the occurrence of stiff inflexed styles (illustrated in Baglin et al., 1972) which apparently exclude foraging birds. Porsch (1935) suggested this as a feature of marsupial-pollinated banksias; he also proposed that the "basket"-like inflorescences in some dryandras were adapted to accommodate the heads of various marsupials (Fig. 8).

The situation in Australia, however, is probably more complex than in South Africa. For example, many of the large, shrubby and even arboreal Proteaceae (and also Myrtaceae) are also visited by nonflying mammals in addition to the cryptic, geoflorous species, yet the latter appear to be better adapted for pollination by nonflying mammals. Most workers probably consider these nonground flowering species to be bird pollinated (e.g., Carlquist, 1974). Admittedly many of the floral characteristics of genera such as *Banksia* do suggest bird pollination. Yet some traits clearly do not. For example, Baglin et al. (1972) state that all *Banksia* inflorescences are odoriferous, yet odor is not associated with ornithophily. Additionally, Morcombe (1968) reports that in *Banksia* nectar secretion is prolific at night, a condition hardly adapted to pollination by diurnal flower birds. Morcombe suggests that the great abundance of nocturnal insects are attracted to *Banksia* inflorescences by the copious nectar, and these in turn are what entices nonflying mammals to the flowers. Considering the highly specialized adaptations of an animal such as the honey possum (see following discussion) for a nectar (and pollen?) diet, it seems unlikely that insects would be the prime attractant, at least for this animal. However, animals such as the southwestern bush rat (a true rodent) might well be attracted by insects. But this would hardly explain why nectar secretion is abundant at night, since insects are highly unlikely pollinators of these flowers. Typically, nectar secretion is synchronized temporally for visitation by the established pollinators coadapted to that particular flower (Faegri & van der Pijl, 1971).



DERIVATION OF CRYPTIC, GEOFLOROUS SPECIES FROM ORNITHOPHILOUS
PROTOTYPES

Various sunbirds and the Cape sugarbird are the typical pollinators of the well-known shrubby proteas in the Cape region with large terminal inflorescences (Fig. 9). However, the cryptic, geoflorous positioning of the inflorescences in sections *Hypocephalae* and *Microgeantheae* must preclude bird pollination, since birds are attracted to flowers visually (Raven, 1972) and odor is not a characteristic of bird-pollinated flowers. In fact, sunbird or sugarbird visits to the cryptic, geoflorous proteas would violate established behavioral patterns in these birds. They are not generally known to frequent the ground, or to explore the dense interior of low shrubs which do not have exposed, colorful flowers.

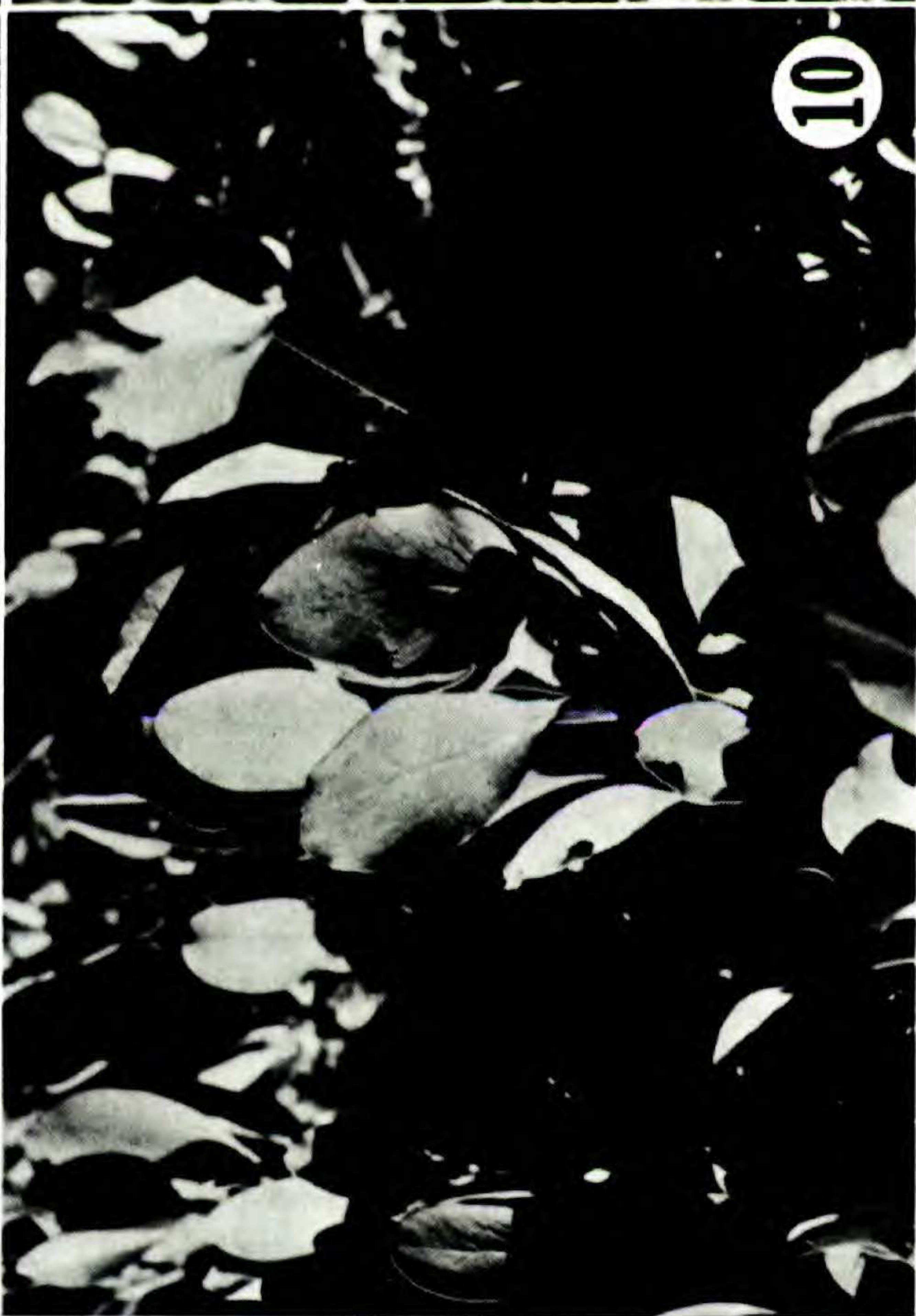
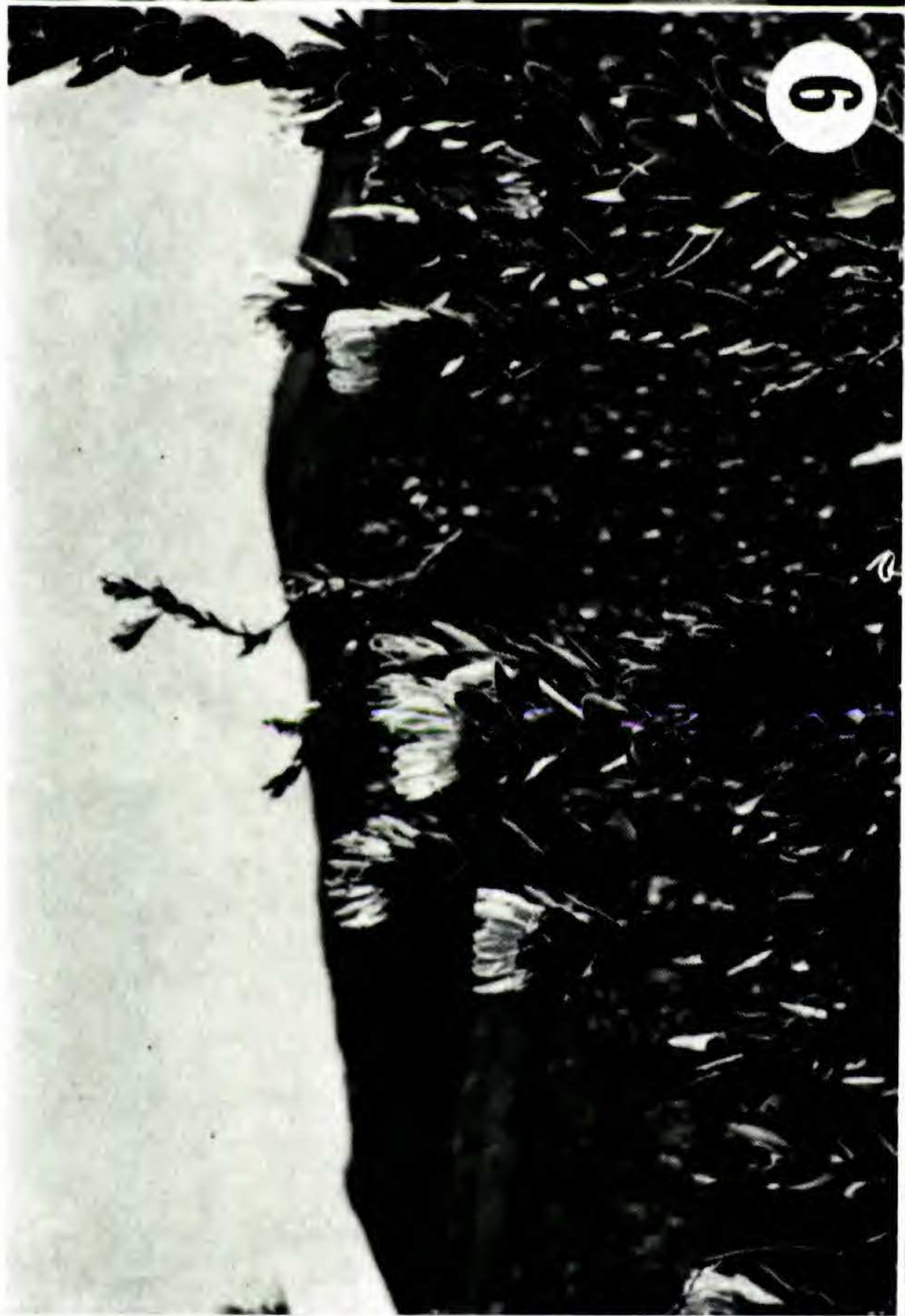
Further evidence that birds are unlikely pollinators of the cryptic, geoflorous proteas is based on observations of *P. nana*. As previously mentioned, this species has pendulous, relatively small (ca. 3 cm wide), dark reddish heads. Initially one might assume that they were bird pollinated. However, a number of flowering plants of *P. nana* were observed in an area densely populated by the orange-breasted sunbird, *Nectarinia violacea* and the Cape sugarbird (*Promerops cafer*) which were feeding freely on several proteaceous shrubs with large terminal heads, and some ericas; however, no birds were observed on *P. nana*. Because the heads are pendulous, flower-visiting birds would probably have to hover to obtain nectar. Sunbirds are capable of hovering (Skead, 1967) but unlike hummingbirds, they hover clumsily. Normally they feed while clasping branches. Nonetheless, in an area with a high density of nectar-feeding birds, a great variety of flowers are normally visited in addition to the preferred species. If sunbirds and sugarbirds showed interest in the flowers of *P. nana*, at least rare visits to these plants would be expected. If nectar-seeking birds are not attracted to *P. nana*, whose inflorescences are visually conspicuous but otherwise generally resemble the cryptic, geoflorous species, it is still more difficult to believe that birds pollinate the latter group. In fact, the great majority of these South African Proteaceae with dark reddish bracts and mostly pendulous flowers might well be pollinated by nonflying mammals.

The cryptic, geoflorous proteas do retain the copious nectar supply typical of bird flowers. They differ from bird flowers, however, by (1) bearing their flowers at or near ground level in a hidden position, (2) emitting a strong "yeast-like" odor, (3) possessing much shorter flowers (ca. 1.5 cm high), and heads of smaller diameter (ca. 4–6 cm wide), and (4) the dull purplish brown coloration of the heads as opposed to the bright, vivid red and/or yellow inflorescences of the bird-pollinated species.

Essentially the same arguments apply to the situation in Australia, except

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FIGURES 5–8.—5. Inflorescences of *Protea subulifolia* at anthesis (same plant as Figs. 1–2).—6. Inflorescences of *Dryandra tenuifolia* at anthesis (same plant as Figs. 3–4).—7. *P. subulifolia* showing chewed succulent bracts and styles (left) and intact inflorescence (right) (near Papias Vlei, Cape Prov., South Africa).—8. *Dryandra* sp., note inflexed styles forming a "basket"-shaped inflorescence (near Perth, West Australia).



that here the predominant flower birds are the honey eaters (Meliphagidae). Likewise in many of the critical genera such as *Banksia*, some species are apparently adapted for bird pollination and others for pollination by nonflying mammals.

Although we believe the cryptic, geoflorous Proteaceae are not pollinated by birds, the system nonetheless appears to have evolved from a bird-pollinated prototype. In addition to some general aspects of the inflorescence and the copious supply of nectar, the nature of the branching patterns associated with inflorescence development also supports the derived nature of the cryptic, geoflorous Proteaceae. The large, shrubby bird-pollinated proteas have terminal inflorescences, whereas the inflorescences in the geoflorous species are largely axillary. These axillary inflorescences are almost certainly derived from terminal inflorescences by progressive stem reduction. Members of the section *Pinifoliae* (which includes *P. nana*) possess intermediate forms in which the stem bearing the inflorescence is greatly shortened. Complete reduction of this stem would give rise to the almost sessile, apparent axillary inflorescences characteristic of *P. subulifolia* and other highly reduced types that occur in the geoflorous sections. Thus morphological evidence supports the proposition that the geoflorous species are derived types originating from bird-pollinated groups. Both L. A. S. Johnson and A. George (personal communications) support the notion that the cryptic, geoflorous Australian Proteaceae are also derived types.

Another interesting example of the apparently derived nature of the cryptic habit occurs in *Protea recondita* Buek ex Meisn. where floral crypsis is accomplished through an entirely different mechanism than geoflory. This species is a low shrub (up to perhaps 1 m high) with terminal inflorescences positioned similarly to the bird-pollinated proteas. The bases of the heads, however, are encircled by a cluster of unusually large, vertically oriented leaves (bracts). These bracts enfold the entire inflorescence (rather like a cabbage!) and, in effect, obscure the head from external view during anthesis (Figs. 10–11).

If the cryptic, geoflorous species of Proteaceae are adapted for pollination by nonflying mammals and were derived from bird-pollinated prototypes, what selective forces might have shifted the system in this direction? The ecological community in which these plants occur provides a possible explanation. Both the Cape region and southwestern Australia are essentially sclerophyllous, fire-adapted shrub communities. In fact, the general aspect of the two communities is remarkably similar, even to the characteristic brownish cast of the vegetation. Furthermore, both regions are extraordinarily rich floristically. Only tropical rainforests are apparently richer in plant species diversity. Both floras are also

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FIGURES 9–12.—9. *Protea compacta*, a typical bird-pollinated species at anthesis (near Papias Vlei, Cape Prov., South Africa).—10. *P. recondita*, shoot with hidden terminal inflorescence at anthesis (Kirstenbosch Botanic Garden, Cape Prov., South Africa).—11. *P. recondita* shoot with terminal inflorescence exposed behind the large, vertical bracts (same plant as Fig. 10).—12. (left) *Banksia media* (from a kodachrome by Alex George, West Australia) inflorescence at anthesis, each rounded point represents one flower, total number of flowers estimated at 4,400. (right) *Banksia* inflorescence with 34 mature fruits.

TABLE 2. Australian mammals known to visit flowers to obtain nectar and/or pollen.

Animal (all marsupials, except <i>Rattus fuscipes</i>)	References
<i>Acrobates pygmaeus</i> (pigmy glider)	Breeden & Breeden (1972), Carlquist (1965)
<i>Antechinus apicalis</i> (dibbler)	Morcombe (1968)
<i>A. flavipes</i> (yellow-footed antechinus)	Breeden & Breeden (1972)
<i>Burramys parvus</i> (mountain pigmy possum)	P. Cook (personal communication)
<i>Cercartetus concinnus</i> (southwestern pigmy possum)	Vose (personal communication), Ride (1970)
<i>C. nanus</i> (eastern pigmy possum)	Baglin et al. (1972), Breeden & Breeden (1972)
<i>Petaurus australis</i> (fluffy or yellow-bellied glider)	Breeden & Breeden (1972)
<i>P. breviceps</i> (sugar glider)	Breeden & Breeden (1970, 1972), Sleumer (1955)
<i>P. norfolcensis</i> (squirrel glider)	Breeden & Breeden (1972)
<i>Phascogale tapvatafa</i> (tuan or Wambenger)	Breeden & Breeden (1972)
<i>Rattus fuscipes</i> (southern bush-rat)	Morcombe (1968)
<i>Tarsipes spencerae</i> (honey mouse)	Morcombe (1968), Glauert (1958), Vose (1971, 1972), Ride (1970).

characterized by nutritionally depauperate soils (Wild, 1968; Loveless, 1961). Insofar as the evolution of the cryptic, geoflorous habit is concerned, however, we believe the fire-adapted nature of these communities is most important.

One way plants can survive burning is to develop rhizomaty. This condition should strongly promote ground flowering. Many, but not all, of the cryptic, geoflorous Proteaceae are rhizomatous. Hence, if rhizomaty has survival value and if there were pollinator competition between bird and nonflying mammals for floral resources, fire and the concomitant development of the rhizomatous habit could have shifted the selective advantage toward nonflying mammal pollination. It is also possible, however, that nonflying mammals, as a result of their generally more aggressive behavior, may have simply out-competed birds as pollinators and hence shifted the selective balance in this way.

A FLORAL CLASS ADAPTED FOR POLLINATION BY NONFLYING MAMMALS AND EVIDENCE FOR COEVOLUTION

Although experimental data are lacking, we believe sufficient circumstantial evidence is available to identify a class of flowers in Proteaceae adapted for pollination by nonflying mammals. Furthermore, this class of flowers has evolved independently at least twice (Africa and Australia) and at least one animal, the so-called honey possum (*Tarsipes spencerae*) has probably coevolved with this floral class in Australia. Furthermore, we believe other animals, particularly some of those in Table 2, may also have coevolved with these proteaceous plants.

The fundamental characteristics we believe might distinguish this floral class include: (1) Inflorescences as the basic units of attraction; generally they are cup-shaped heads (spikes in *Banksia*). (2) Heads typically hidden deep within the foliage, often at or near ground level; if exposed (as in *Banksia*) then with (a) structural modifications, such as stiff incurved styles or (b) nocturnal

rhythms of nectar production and/or anthesis to preclude successful nectar foraging by birds. (3) Heads about 2–8 cm wide with perhaps 100–200 flowers (several thousand in *Banksia*), and strongly attached to stems. (4) Heads producing a copious nectar supply; in some proteas also possessing apparent food bodies in the form of soft, fleshy bracts and styles acting as complementary attractants. (5) Heads odoriferous; we characterize these as “nutty” or “yeasty” in *Protea*; Porsch (1935) suggests “sour milk” and “caraway liquor” for *Dryandra*. (6) Heads with reddish brown to purplish bracts, individual flowers mostly whitish. (7) Temporal spacing of anthesis in the inflorescence, thereby limiting the number of simultaneously open flowers in the head to no more than several of the outer whorls.

Most of these characteristics were discussed previously and need no further elaboration. The most obvious feature of this putative floral class is its basic resemblance to bat-pollinated flowers (cf. Faegri & van der Pijl, 1971). The primary differences are the cryptic, geoflorous habits and the compound inflorescence as the attracting unit. There are apparently also structural modifications of the styles in the Australian species to discourage bird foraging. The basic similarities to bat flowers, however, should not be surprising since the apparent pollinators are all small mammals with perhaps generally similar energetic requirements and sensory systems [Faegri & van der Pijl (1971) point out that echo location is only poorly developed in the flower-feeding bats, Megachiroptera].

One of the strongest lines of indirect evidence supporting the idea of a class of flowers pollinated by nonflying mammals in South Africa and Australia revolves about the convergent nature of the floral characteristics in these two subfamilies of Proteaceae. If one examines the pollination syndrome of any flower class, they have essentially the same general features over the entire world. Thus convergent evolution for floral structure and habit is a necessary product of any widespread pollination system.

The variations in floral habit and structure among the Proteaceae putatively pollinated by nonflying mammals therefore reflect differences in (1) modes of locomotion to the flowers (i.e., terrestrial or arboreal movements as opposed to flying) and (2) foraging behavior. The great mobility of the nonflying mammals around flowers and the highly developed chewing apparatus (particularly among generalized feeding rodents) would probably make an attracting unit consisting of a single, large flower nonadaptive because of the destructive nature of these animals. The Proteaceae have apparently compensated for the highly destructive activities of these apparent pollinators by increasing the number of reproductive units far beyond what is necessary to maintain successful reproductive levels. In the South African cryptic, geoflorous species seed set is consistently low, usually below 5%. The same is true in the corresponding Australian genera (A. George, personal communication). In *Banksia*, the number of flowers per spike probably exceeds 4,000, yet the mature fruits are so large that it would be a physical impossibility for more than perhaps 50 to develop (Fig. 12). In addition to maximizing flower production, the flowering patterns in the heads are staggered temporally so that only several outer whorls are in anthesis simultaneously. If all the flowers opened concurrently, and in view of their sweetness

at anthesis, the entire inflorescence might be more easily destroyed by attracting a large number of pollinators.

If generalist feeding, nonflying mammals are potentially so aggressive and opportunistic in exploiting food sources, one might ask why they rarely disturb the typically bird-pollinated South African proteas. First, the bird-pollinated species are not odoriferous and the terminal inflorescences are typically borne high above ground level (Fig. 9); thus most such inflorescences probably escape detection. Another aspect, however, is the presence in some species (especially section *Speciosae*) of a thick layer of trichomes over the top of the heads. Such a dense layer of trichomes might serve to discourage mammals from chewing to the base of the heads where the nectar is located and thus act as a kind of "mammal guard." Birds, of course, easily probe through this layer with their long bills. The heads are also closely surrounded by stiff leathery bracts, which also have considerable trichome development along their margins, where chewing is most apt to be initiated. Excellent illustrations of these phenomena are found in Rousseau (1970). Finally, the acrid taste of these bracts, as opposed to the sweetness of the bracts and styles in the cryptic, geoflorous species, might also be important.

Many observations of nonflying mammals on Proteaceae (and also Myrtaceae) are reported in the popular natural history literature of Australia, e.g., Serventy & Raymond (1974) and Russell (1974) (see also references in Table 2). In fact, so prevalent are these observations that many Australian biologists take this pollination system essentially for granted (Morcombe, 1968; Johnson & Briggs, 1975). To our knowledge, however, no definitive data to establish this relationship has yet been published. Of the nonflying mammals listed in Table 2 as potential pollinators, the honey possum or noolbenger (*Tarsipes spencerae*), appears to be the best known and apparently the most highly specialized for nectar (and pollen?) feeding. This amazing animal was studied in captivity by Glauert (1958) and Vose (1972, 1973), who include illustrations. Because no comprehensive review of its spectacular adaptations for nectar (and pollen?) feeding is evidently available, a brief resumé of these characteristics taken from the sources quoted above and from Carlquist (1965) might be useful.

The head and body are small (6–8 cm long and weighing only 7–11 g). The elongated, tapering snout composes two-thirds of the head. The ears are set far back on the head and the nose is grooved. These features no doubt allow the honey possum to probe deeply into flowers. The tail is longer than both the head and body (8–10 cm) and is prehensile, while the digits of the limbs are slender and elongated for grasping; both characteristics being excellent modifications for the arboreal habit. But it is in the mouth where the most fascinating adaptations for nectar (and pollen?) feeding exist.

The tongue is extensible to twice its normal length, tapered, slightly serrated on the margin and brushed at the tip (Fig. 2 in Vose, 1972). It is exerted through a funnellike structure at the tip of the tapering snout where the lips are modified into flanges. The palate is characterized by ridges which apparently remove accumulated nectar (and pollen?) from the tongue when it is retracted. The jaws are much reduced and dentition rudimentary. Only the upper canines and lower incisors are developed and these appear to function largely in orienting

the tongue during retraction. There is no caecum, such a digesting organ for solid food apparently being superfluous in an animal adapted to a nectar diet. Additional structural and especially physiological adaptations for nectar (and pollen?) feeding will no doubt be discovered when more extensive studies are conducted. The evidence that *Tarsipes* is adapted to a diet derived from flowers (and probably occasional insects) is overwhelming. As a corollary, the conclusion that *Tarsipes* has coevolved as a pollinating agent with various proteaceous (and myrtaceous) genera is inescapable.

Sleumer (1955) states that in both northeastern Australia and southeastern New Guinea, the sugar glider (*Petaurus breviceps*), along with several flower birds, are always associated with flowering *Banksia dentata* and the myrtaceous genera *Melaleuca* and *Eucalyptus*. According to Sleumer, the sugar glider sucks nectar with a "wormshaped" tongue, suggesting possible anatomical adaptations for a nectar diet.

Although reference has so far only been made to the cryptic, geoflorous proteas, other Australian proteaceous and myrtaceous genera such as *Eucalyptus* and *Melaleuca* are known, or suspected, to be visited by various nonflying mammals. For example, *Tarsipes* reportedly feeds on *Hakea* and *Beaufortia* (Morcombe, 1968). Vose (1972) also lists species of *Callistemon* and *Grevillea* from which *Tarsipes* will extract nectar in captivity. Additional reports of nectar sources for flower-visiting marsupials include *Dryandra* (Glauert, 1958) and *Angophora* (Porsch, 1934).

If the honey possum and possibly also other small arboreal marsupials have apparently coevolved in Australia, why has coevolution between Proteaceae and true rodents not occurred in South Africa? One obvious reason is that the proteas in South Africa ostensibly pollinated by nonflying mammals do not flower throughout the year. The flowering period for these plant groups is limited primarily to late winter or early spring, as previously mentioned. Thus coevolution is impossible because the flowers do not provide a constant food source for these animals which are active throughout the year. Furthermore, it is likely that plants can adapt relatively easily to a generalized feeder, such as many rodents, and that pollination can be reasonably well assured by offering high rewards and reducing competition with other food sources in the community by flowering at the low point in the food cycle.

POTENTIAL POLLINATION BY NONFLYING MAMMALS IN OTHER PLANT GROUPS

Discussion in this paper is confined essentially to the possible pollination of Proteaceae by nonflying mammals in South Africa and Australia because we observed many of these species and genera in the field. In any overall consideration of the phenomenon, however, other plant groups should not be overlooked. If pollination by small, arboreal marsupials occurs in Australian Proteaceae, it probably also occurs in Myrtaceae. The mouselike lemurs on Madagascar (Sussman & Tattersall, 1976) which take nectar from introduced kapok must be adapted for visiting similar indigenous flowers as well. Porsch (1935) mentions Madagascan *Symphonia* (Guttiferae) as a possible flower adapted for pollination by

nonflying mammals. He also discusses other families, e.g., Bombacaceae and Lecythidaceae, which also might have adaptations for pollination by various nonflying mammals. Porsch's observations merit careful reconsideration, and, especially, critical field studies to test his hypotheses.

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